

On Some Living and Fossil Volutes  
 Referred to *Miomelon* Dall, 1907  
 and *Proscaphella* von Ihering, 1907

BY

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(4 Plates; 3 Text figures)

## INTRODUCTION

THE FAMILY VOLUTIDAE is well known to collectors and amateurs because of the size and beauty of its representatives. It is equally important from the taxonomic and phylogenetic points of view, although its relationship with closely related families is still unclear. Evolutionary trends and phylogenetic branching within the family have only recently begun to be properly understood, mostly through anatomical work. Unfortunately, most of this work has not been complemented with studies of fossil material.

The recent revision of the family by WEAVER & DUPONT (1970) has contributed to the understanding of this group by compiling the available facts and providing new information on the living species. Yet, many species and particularly genera remain still insufficiently known to evaluate conflicting interpretations as to their true relationships to other species or genera and to their position within the proposed subfamilial ranking.

The genus *Miomelon* Dall, 1907, represented by two Recent species from off the central part of Chile and the southern tip of southern South America is one of the genera in question. Information provided in this paper intends to clarify current taxonomic views on this genus.

1. The Living Species of *Miomelon*

The genus *Miomelon* was originally proposed by DALL (1907) as a "section" of the genus *Adelomelon* Dall, 1907,

to include the living species *Volutilithes philippiana* Dall, 1889 (Figure 1) taken by the *Albatross* (Station 2791) in lat. 38°08'S and long. 75°53'W off the southwest coast of Chile, in 677 fms (1238m), mud. Several fossil species from the Tertiary strata of central Chile were also referred by Dall to his "section."

Seemingly, it was WENZ (1943) who first gave generic status to *Miomelon*. Later on, POWELL (1951) briefly discussed it when describing the new species *M. scoresbyana* taken "... between Falkland Is. and the Strait of Magellan, 59°09'45''S., 64°56' W. ... in 150m."



Figure 1

*Miomelon philippiana* (Dall, 1889)

Holotype, U. S. N. M. 97128; lat. 38°08'S; long. 75°53'W; 677 fathoms; 36.5 mm high

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Recently, WEAVER & DUPONT (1970: 131) enlarged the diagnosis of the genus *Miomelon*; nonetheless, its position within the Volutidae remains uncertain. Authors have suggested its inclusion in 2 different subfamilies (PILSBRY & OLSSON, 1954; CLENCH & TURNER, 1964; WEAVER & DUPONT, 1970), but except for the figure of a rachidian tooth of the type specimen of *M. philippiana* (PILSBRY & OLSSON, *op. cit.*, pl. 3, fig. 9) there has been no satisfactory discussion of the characteristics of the genus.

The status of the 2 known species is equally conflicting. Purported samples of *Miomelon philippiana* (Dall, 1889) were recently recorded by WEAVER (1964: 2 photographs; WEAVER & DUPONT (1970) and REHDER (1970). *Miomelon scoresbyana* Powell, 1951, a species with several atypical generic features, has not been found again.

Thanks to the interest of Mr. Elias Alarcón of the Chilean Instituto de Fomento Pesquero we have been able to study samples of a new species of *Miomelon* found off the central coast of Chile to which all the above mentioned Recent records of *M. philippiana* seem to belong.

The study of the shell and soft parts of this species, named here in honor of Mr. Alarcón, permits a better understanding of the generic characteristics. Descriptions of the genus and the new species follow:

#### *Miomelon* Dall, 1907

*Adelomelon* (*Miomelon*) Dall, 1907, Smithsonian Misc. Coll. 48 (3): 365 (Febr.). Type species *Volutilithes philippiana* Dall, 1890, by OD

*Miomelon* Dall. WENZ, 1943, Handb. Paläozool. 6 (1), Gastropoda: 1350, text fig. 3823; POWELL, 1951, Discov. Reprt. 26: 163; PILSBRY & OLSSON, 1954, Bull. Amer. Paleont. 35 (152): 289, pl. 27, fig. 9 (radular tooth); WEAVER & DUPONT, 1970, Living Volutes: 131; text fig. 29, pl. 56, figs. C, D, E, F

**Range of Distribution:** Off the northern coast of Chile to the Falkland Islands; 110 to 1238 m.

**Diagnosis:** Shell obovate, up to 90 mm in height; densely axially folded and with spiral striae or costae; with or without costellae in the interspaces; spire elevated, almost as long as the aperture and somewhat excavated in front of the suture. Protoconch minute, usually eroded, not conspicuously differentiated from the succeeding whorls. Columellar plaits few (3-4), oblique, often duplicated. Periostracum thin. Animal devoid of operculum and with (or without?) eyes. Foot moderately pointed behind, in front auriculated at the corners and double edged. Head very wide with lateral expansions. Verge situated just behind the right tentacle; small, clavate, with a smaller conical distal appendix. Siphon long and voluminous with a large left appendage in the adult. Radula with tricuspid teeth.

*Miomelon* appears to be closer to *Tractolira* Dall, 1896, than to any other genus of the Volutidae.

*Miomelon alarconi* Stuardo & Villarroel, spec. nov.

(Figure 1 and Figures 4a, 4b, 5a, 5b)

*Miomelon philippiana* (Dall). WEAVER, 1964, Hawaii. Shell News 12 (5): 8, upper right text fig.; WEAVER & DUPONT, 1970, Living Volutes: 132, pl. 56, figs. E, D, fig. 29; REHDER, 1970, Proc. Biol. Soc. Wash. 83: 594 (*non* DALL, 1889)

**Description:** Shell medium sized, elongated, fusiform; whitish with a thin ash-purple periostracum. Whorls 6, convex, but with a concave ramp below the suture. Spire as long as the aperture. Aperture half-moon shaped, slightly constricted on its lower part to form a wide canal. Suture as in the type of the genus, deeply and narrowly channeled. Outer lip thin, sharp, very weakly liriate

### Explanation of Figures 4 to 8

*Miomelon alarconi* Stuardo & Villarroel, spec. nov.

Figures 4a, 4b: Holotype, MZICB 5553; Chanco Bay; 89.7 mm high

Figures 5a, 5b: Juvenile, paratype, MZICB 5555; Achira Point - Nugurue Point; 39.5 mm high

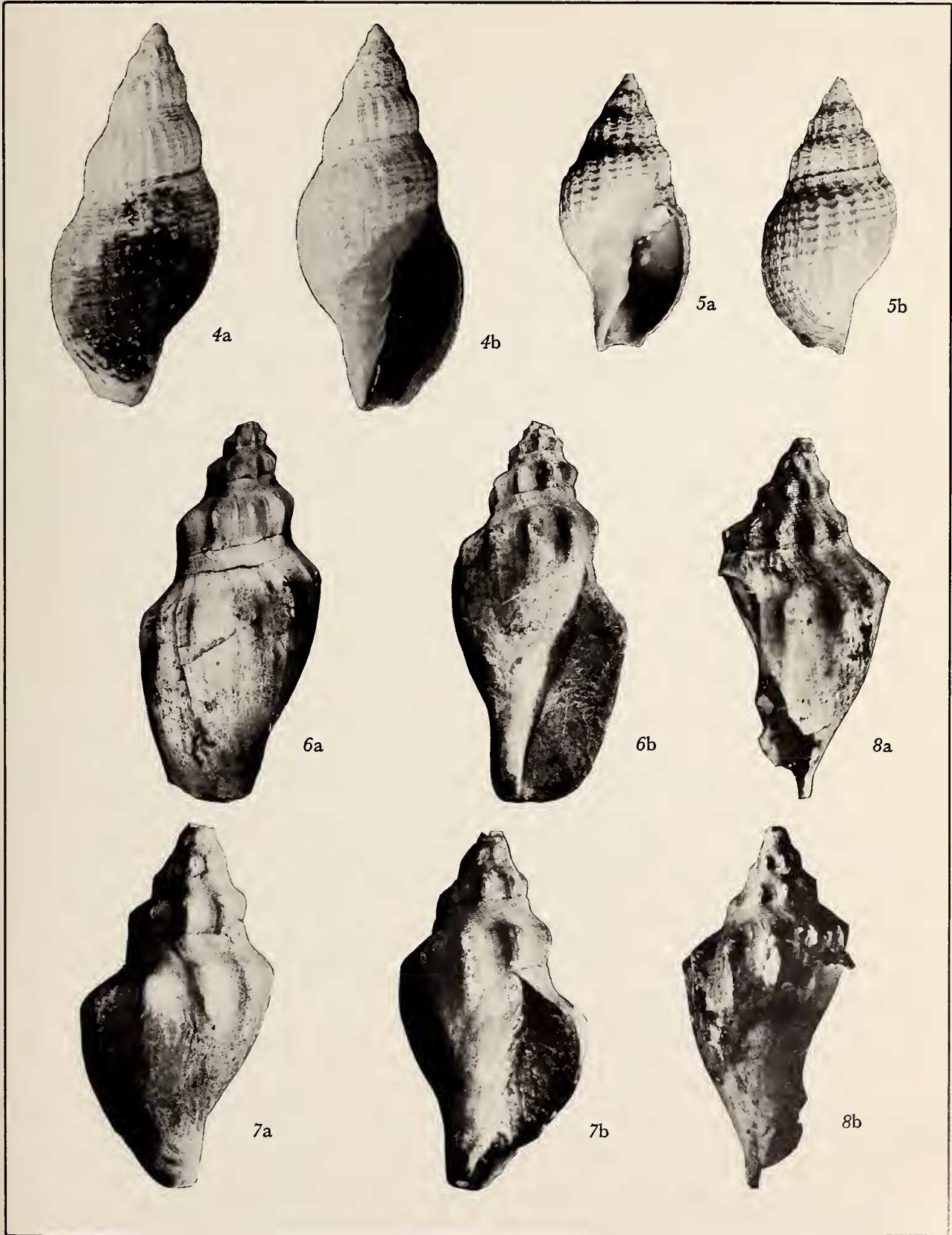
*Proscaphella taverai* Stuardo & Villarroel, spec. nov.

Figures 6a, 6b: Holotype, MNHN 107; Tertiary, Ranquil, Ancud; 79.5 mm high

Figures 7a, 7b: Paratype, MNHN 112; Lower Miocene, Navidad; 44.3 mm high

*Proscaphella* sp.

Figures 8a, 8b: MZICB N/52 CP; Lower Miocene, Navidad; 50.8 mm high





internally; inner lip excavated; parietal glaze and inner part of the outer lip light-brown to orange-brown in color; anterior notch broad, not differentiated. Columella thin, nearly straight, with 3 or 4 more or less equally spaced columellar plaits, often duplicated by a thinner replica. The anteriormost plicae strongest.

Axial sculpture consisting of regularly spaced, well developed folds becoming somewhat obsolete in the last (body) whorl, and numerous very fine axial striae; folds and striae well marked in the juveniles, less conspicuous in the adults. Spiral sculpture formed by well marked costae separated by interspaces as wide or wider than the costae. There is a variable number of costellae present on the last whorl.

Protoconch eroded, short.

#### Measurements (in mm)

	Height	Width	Aperture
Holotype (MZICB 5553)	89.7	39.4	46.6
Paratypes (MZICB 5554)	82.3	35.0	45.4
(MZICB 5554)	79.7	36.9	42.3
(MZICB 5554)	85.9	40.0	46.2
(MZICB 5554)	78.4	38.1	44.0
—	80.0	36.0	45.7
—	84.9	37.6	48.7
(MZICB 5555)	39.7	10.0	24.5
(MZICB 5556)	79.3	37.0	45.7
(MZICB 5556)	63.1	30.0	35.3

**Type Locality:** Chanco Bay (35°45'S; 72°34'W) in 125 m; on flagstone.

The holotype (MZICB 5553) and 6 paratypes (MZICB 5554) were collected at this locality on the 4<sup>th</sup> of February, 1970. Two of the remaining paratypes (MZICB 5556) were dredged at lat. 37°51'07"S; and long. 73°52'06"W in 205 m, and the juvenile (MZICB 5555) was obtained between Punta Achira (36°41'S; 74°49'W) and Punta Nugurue (35°58'S; 72°47'W) at 335 m.

WEAVER & DUPONT (1970) recorded this species from off Coquimbo, in 60 to 80 fathoms (110-150m) and REHDER (1970) from off Valparaiso, in 200m.

#### REMARKS

**The Shell:** POWELL (1951: 163) described his new species, *Miomelon scoresbyana*, with a short spire and almost obsolete sculpture consisting of very numerous but weak axial growth lines and equally numerous subobsolete spiral threads. Notwithstanding these features, the species was included in the genus *Miomelon* because of the "form of the suture, the plaits, absence of a columellar plait, weak,

broad anterior notch and ill-defined fasciole." However, its inclusion in the genus as understood here, seems to us questionable.

No specimens of *Miomelon philippiana* Dall have been available to us and we have not seen the type. Nonetheless, the figure and the description of the shell given by Dall show distinct differences.

The single specimen studied by Dall was only 36.5 mm in height (Figure 1) and as he suggested, it was probably not fully adult. Thus, a comparison of the shell features of *Miomelon philippiana* with those of the new species would seem difficult since the adult specimens of the former are not known. However, juveniles of the new species the same size as the holotype of *M. philippiana* are quite different in shell characteristics. The identity of the young with the adults of the new species cannot be doubted even if shell features only are considered; a comparison of Figures 4 and 5 shows that the shell characters of *M. alarconi* do not vary with age. This is probably also true of *M. philippiana*. Furthermore, the identity of juvenile with adult *M. alarconi* is fully corroborated on the basis of the soft parts.

The main shell differences for each species can be outlined as follows:

*Miomelon philippiana* was described as having a dark olivaceous-ash color; 6 whorls, with probably 1 or 2 more when adult; sculpture formed by coarse grooves which become finer, almost linear anteriorly on the last whorl, and flattened narrow interspaces wider than the grooves. Its aperture is narrow, pointed behind, with the outer lip not lirate internally.

*Miomelon alarconi* has an ash-purple periostracum; 5½ whorls in the juvenile and only 6 whorls in the adult stages; sculpture of rounded costae, separated by interspaces with costellae; a rather wide half-moon shaped aperture and an outer lip weakly lirate internally.

Dr. H. A. Rehder who very kindly compared one of our paratypes and shells of this same species deposited in the Smithsonian Institution's collections with the type of *Miomelon philippiana* wrote to us:

"The type of *M. philippiana*, which measures 36 mm in length, has about 5¾ whorls (the early whorls are worn), is more slender, the last whorl not as convex as the new species. The spiral sculpture is finer with the threads more numerous. One of our specimens of the new species, also about 5¾ whorls, measures 50 mm in length."

**The external anatomy:** The external anatomy of the two previously known species has been described in more or less detail. That of *Miomelon philippiana* was described by DALL (1889: 315) as follows:

"The exterior of the body is of a yellowish color and, as contracted in alcohol, rather rugose; the foot is moderately

pointed behind, in front auriculated at the corners and double-edged; there is no operculum or rudiment of an opercular gland; the head is wide, with rather long, rounded, moderately stout tentacles with an expansion at the outer bases, but no eyes in the specimen before me. The siphon is long and has an appendix near its base on each side of the gutter; the gill and osphradium are as usual; the anus is simple, not free or prominent; near it are a purpuriferous and a large slime-gland, on the dome of the mantle; the verge is small, clavate, with a smaller conical tip, not flattened, about as long as one of the tentacles but thicker. It is situated immediately behind the right tentacle."

Regarding the general external appearance of *Miomelon scoresbyana*, POWELL (1951) stated that the foot is long and tapered and the long and tapered tentacles (10mm) have eyes at the outer side of the bases. To explain the lack of eyes in the type of the genus he further suggested that it could be due to "the much greater depth at which it was taken (677 fms)." Unfortunately, this author did not study the radula, mistakenly minimizing its importance.

The soft parts of 3 preserved specimens of the new species were available to us. Their rather hard condition prevented a detailed study of the internal anatomy. However, the external characteristics could be observed in some detail, allowing comparison with the above mentioned observations by Dall and the anatomical details published for the genera *Adelomelon*, *Voluta*, *Odontocymbiola* and *Volutocorbis* by WOODWARD (1900), PACE (1902) and CLENCH & TURNER (1964).

The body of *Miomelon alarconi* is of a brown-reddish coloration in alcohol and the foot has the characteristics of the species of Dall, lacking also an operculum.

The head is very wide, appearing divided in the adult by a frontal furrow or furrow-like fold in a symmetric position (Figure 2B). In the juvenile this furrow is not observed, indicating that it probably is only an artifact of fixation. The tentacles are stout and moderately long.

Most conspicuous are the lateral auricular expansions or flaps, located at the outer bases of the tentacles, extending the head laterally. Each one of them bears on its proximal part an eye located on a small papilla.

The siphon is rather long and voluminous and, in the adult, its appendages are of very unequal size, as described for *Voluta musica* by PACE (1902: 22) and CLENCH & TURNER (1964: 139; plt. 83, fig. 3). The appendage on the right side is small, tongue-shaped (Figure 2B, 2), lying on the inner part of the mantle border; the left appendage is as broad as the inner diameter of the siphon arising about half-way along it and almost reaching its extremity. In the juvenile, the left appendage is about as small as the right one, demonstrating that the size relationship of the appendages changes with age.

There is no observable verge in the specimens at hand. The mantle edge is thin, having neither papillae nor pigment.

The pallial cavity is wide and the organs of the pallial complex resemble, in general, those of other volutids.

The ctenidium is long and the filaments are wide, triangularly elongated and unpigmented. The bipectinate osphradium is well developed and darkly pigmented. The hypobranchial (mucous) gland appears, on the other hand, less developed, being represented by only a few folds. The positions of the anal, female genital, and kidney openings are as usual (Figure 2A, 16).

**The internal anatomy:** Internally, the arrangement of the ganglia in the circum-oesophageal collar closely resembles that of *Adelomelon ancilla*.

The digestive tract was examined in detail prior to the removal of the radula. Its morphology agrees in general with the characteristics referred to the subfamily Zidoninae H. & A. Adams by CLENCH & TURNER (1964). The proboscis or introvert was retracted in the 3 specimens studied, appearing as a large oval-elongated mass. The salivary glands resemble in form and distribution the scheme drawn by CLENCH & TURNER (*op. cit.*) for the Zidoninae. Both the racemose and the tubular glands

### Explanation of Figures 9 to 11

#### *Proscaphella obesa* (Philippi, 1887)

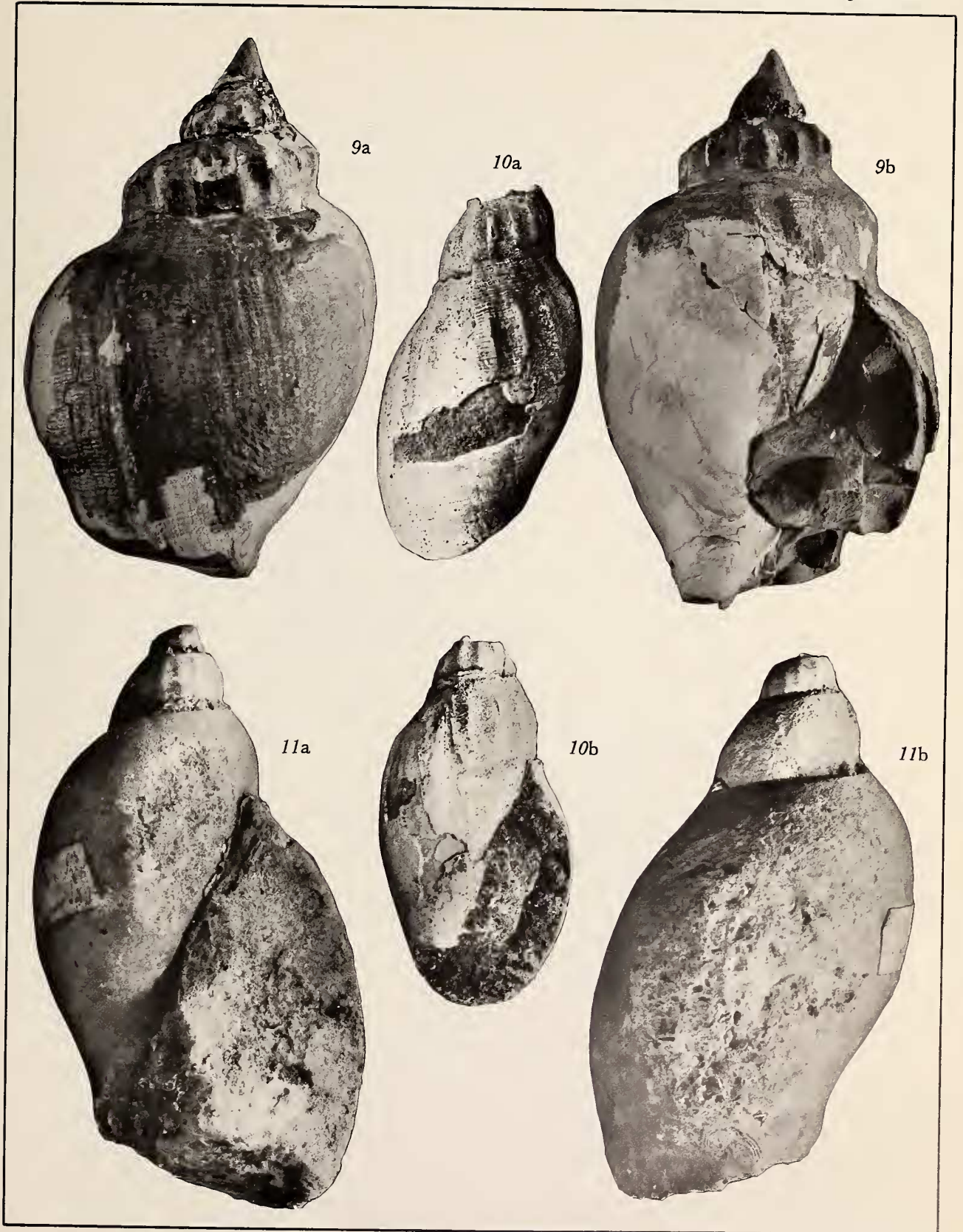
Figures 9a, 9b: MZICB IM/120; Miocene, northern part of Mocha Island; 117.7 mm high

#### *Proscaphella gracilior* (von Ihering, 1896)

Figures 10a, 10b: Holotype, MNHN 105; Middle Miocene, Santa Cruz, Argentina; 37.2 mm high

#### *Proscaphella dorbignyana* (Philippi, 1887)

Figures 11a, 11b: Holotype, MNHN 104; Middle Miocene, Santa Cruz, Argentina, 118 mm high







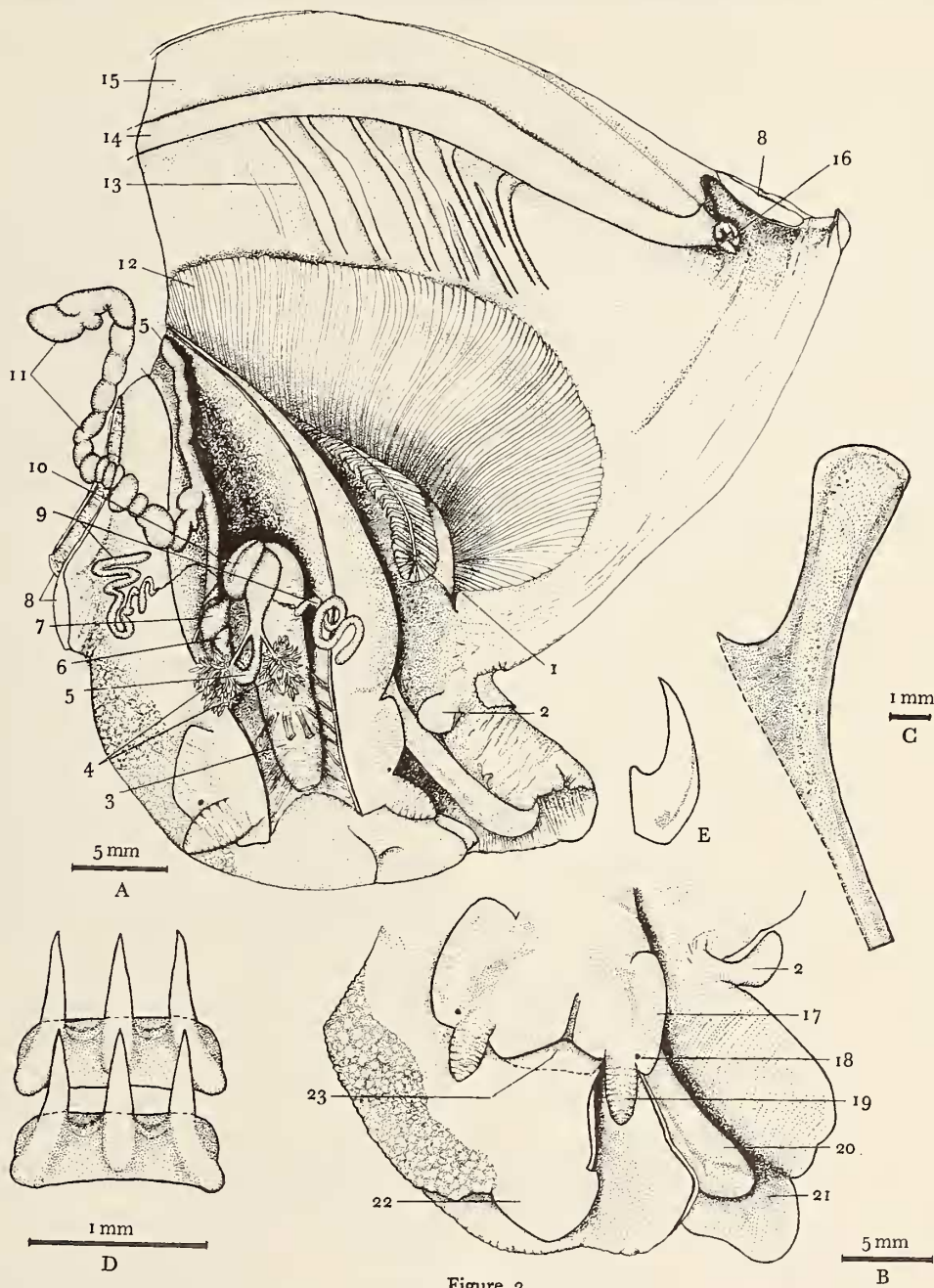


Figure 2

*Miomelon alarconi* Stuardo & Villarroel, spec. nov.

- A. - Anatomical dissection of the anterior half of a female specimen (paratype) with the proboscis retracted.  
 1 - osphradium    2 - right siphonal appendage    3 - introvert  
 4 - racemose "salivary glands"    5 - oesophagus  
 6 - valve of Leiblein    7 - circum-oesophageal ring  
 8 - columellar muscle and mantle edge attachment  
 9 - tubular salivary glands    10 - radular sac  
 11 - Leiblein's glands or oesophageal caecum    12 - ctenidium

- 13 - hypobranchial or mucous gland    14 - rectum  
 15 - oviduct    16 - anus  
 B. - Head of the same specimen, showing:  
 17 - lateral auricular expansion    18 - eye;    19 - tentacle  
 20 - siphon    21 - foot    22 - mouth  
 The siphon is laid open to show left siphonal appendage  
 C. - Ctenidial filament  
 D. - Frontal view of two teeth in normal position  
 E. - Side view of single tooth

cover the posterior part of the introvert as well as part of the oesophagus and the radular sac. The thin and straight ducts of the racemose glands are placed near the base of the introvert and run parallel to the oesophagus, opening close to the aperture. The tubular glands have their distal ends loosely entangled with the racemose glands, but throughout the major part of their length they appear free and convoluted, becoming progressively finer. They meet at the posterior end of the buccal mass, under the radular sac, forming a fine, delicate duct which continues forwards. Due to the hardened condition of the specimens examined we were unable to determine the point where the duct enters the buccal cavity and its subsequent course. Whether this pattern differs from the general model given for the Zidoninae or not, cannot be ascertained at the moment.

Immediately after leaving the introvert, the initial segment of the oesophagus forms a short thin-walled crop-like enlargement which, in turning sharply to the right, diminishes again in diameter. From here, the oesophagus continues forward, forming a straight segment where the racemose glands open. It then makes another sharp turn back and downward, becoming somewhat enlarged and thick-walled (valve of Leiblein) till reaching the circumoesophageal ring.

A crop-like structure similar to that found in *Miomelon alarconi* was described and figured for *Provocator pulcher* by BARATTINI & URETA (1965, pl. 5, fig. 3). PACE (1902) and WOODWARD (1900) also referred to an oesophageal enlargement in *Neptuneopsis gilchristi* Sowerby and *Adelomelon ancilla* (Solander), remarking, however, that it was thick-walled in the former and "appeared" to be more muscular in the latter. Dissection of the digestive tract in specimens of *A. ancilla* from the Magellan Strait did not show this enlargement, casting doubt on the constancy of this character. CLENCH & TURNER (1964) did not mention it. The Leiblein's gland does not seem to be proportionally as long as in the Zidoninae.

The radula and the rachidian teeth of *Miomelon alarconi* agree, in general, with the figure given by PILSBRY & OLSSON (1954, pl. 3, fig. 9) for *M. philippiana* Dall.

We counted from about 59 to 62 rows of large tricuspid teeth whose denticles (cusps) are widely separated yet united at their bases. Moreover, the cusps are curved downwards and the tops of the 2 lateral ones are conspicuously curved inwards.

Pilsbry & Olsson's figure seems too simplified as the 3 denticles appear completely separated. However, they correctly remarked that these denticles are "slender curved, fang-like, seated on a flattened base" (PILSBRY & OLSSON, 1954: 280). The basal plate is almost rectangular with rather straight anterior and posterior borders; the base of

the denticles is not located in the same plane as the basal plate forming an almost right angle with it (Figure 2, D and E).

It seems of interest to point out that this type of tooth somewhat resembles the characteristics of the rachidian tooth of the Odontocymbiolinae and of at least some Zidoninae, suggesting a transitional stage as discussed further below. This similarity, however, might only be the result of convergence since *Miomelon alarconi* presents also other characteristics of its soft parts considered typical for other subfamilies. For instance, the lobes on the base of the siphons are of very unequal size resembling the same feature described by Clench and Turner for the Volutinae. Since *Miomelon* cannot be included in the Volutinae, the use of this feature at the subfamily level should be carefully considered. Its phylogenetic value seems doubtful.

The presence of a furrow or furrow-like fold in the adults of this species is a puzzling feature. It is probably formed by the contraction of the wide frontal border of the head, but it might also be the equivalent of an incipient stage of the deep median cleft described by WOODWARD (1900) in *Volutocorbis abyssicola* (placed in the subfamily Athletinae by Pilsbry & Olsson) and mentioned also by CLENCH & TURNER (1964) for the Scaphellinae. Finally, the apparent reduction in the size of the hypobranchial gland might denote a tendency to eliminate the gland as it has happened in *V. abyssicola* as a result of adaptation to depth, perhaps to improve ventilation or for some other reasons. To decide if these apparent analogies do represent phylogenetic trends, a great deal of more information on the anatomy and distribution of the other genera is needed.

It has been suggested that the combined study of the radula and the anatomy of the soft parts might indicate true relationships and evolutionary trends in the Volutidae. The study by Clench & Turner has contributed a great deal to demonstrate it; however, as often happens, both might involve mosaic tendencies impeding taxonomic correlations at the subfamily level.

Pilsbry & Olsson have pointed out that the triserial radula of *Volutocorbis* Dall, 1890 (1·1·1) is evidently a more primitive condition than the 0·1·0 radula normally present in volutes. Aside from *Volutocorbis*, triserial teeth were found in *Benthovoluta* (subfamily?), *Microvoluta* Angas, 1877 and *Volutomitra* H. & A. Adams, 1853 (Volutomitrinae of authors); nonetheless, while *Volutocorbis* has a rachidian tooth of the tricuspid "volutoid" type, *Microvoluta* and *Volutomitra* present one of the "scapheloid" type, deeply biramosed and wishbone-like. It would then seem that there is not one but at least two or more primitive types of triserial radula from which the differ-

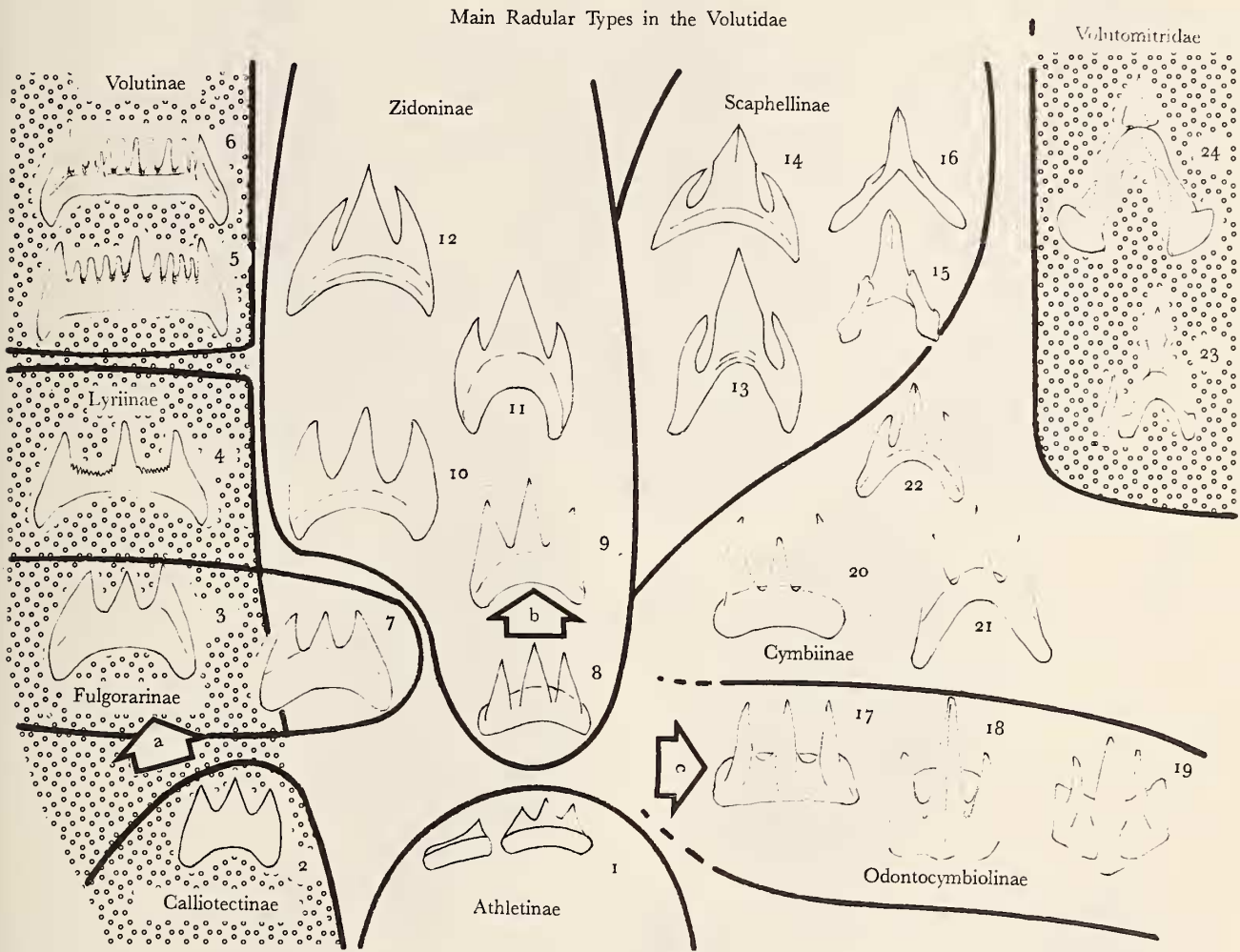


Figure 3

Possible adaptive trends of the radular types in the Volutidae  
 Shaded areas indicate presence of operculum. All suggested trends  
 are not necessarily phylogenetic

- 1 - *Volutocorbis* (Athletinae)
- 2 - *Calliotectum* (Calliotectinae)
- 3 - *Lyria*, *Festilyria* (Lyriinae - Fulgorarinae)
- 4 - *Lyria* (Lyriinae)
- 5 - *Voluta* (Volutinae)
- 6 - *Voluta* (Volutinae)
- 7 - *Fulgoraria* (Fulgorarinae)
- 8 - *Adelomelon* (Zidoninae)
- 9 - *Adelomelon* (Zidoninae)
- 10 - *Zidona* (Zidoninae)
- 11 - *Provocator* (Zidoninae)
- 12 - *Adelomelon* (Zidoninae)
- 13 - *Aurinia* (Scaphellinae)

- 14 - *Volutifusus* (Scaphellinae)
- 15 - *Scaphella* (*Clenchina*) (Scaphellinae)
- 16 - *Scaphella* (Scaphellinae)
- 17 - *Miomelon* (Odontocymbiolinae)
- 18 - *Volutoconus* (Odontocymbiolinae)
- 19 - *Odontocymbiola* (Odontocymbiolinae)
- 20 - *Cymbium* (Cymbiinae)
- 21 - *Cymbiolacca* (Cymbiinae)
- 22 - *Cymbiola* (Cymbiinae)
- 23 - *Microvoluta* (Volutomitridae)
- 24 - *Volutomitra* (Volutomitridae)

(Drawings adapted from PILSBRY & OLSSON, 1954; CLENCH & TURNER, 1964; WEAVER & DUPONT, 1970; CERNOHORSKY, 1970, and BAYER, 1970; No. 17 is original)

ent types of rachidian teeth in the Volutidae might have evolved.

BAYER (1971: 216) claims that "... the form of the rachidian tooth in the Volutomitrinae speaks strongly for its inclusion in the family Volutidae, perhaps even in the subfamily Scaphellinae." However, CERNOHORSKY (1970) has proposed to elevate the Volutomitrinae to family rank, considering that it is intermediate in characters between the Volutidae and the Mitridae. The continuous record of this group from Early Paleocene or Late Cretaceous times to the present day, the presence of opercula in almost all living genera and a radular formula  $1 \cdot 1 \cdot 1$  or  $0 \cdot 1 \cdot 0$  justify Cernohorsky's conclusion.

Undoubtedly, convergence is present in several cases within the patterns of radular adaptation reached by different groups in the Volutidae. In fact, similarities can be observed not only among different subfamilies but in different families as well, as the detailed study of the radula of the Mitridae made by CERNOHORSKY (*op. cit.*) proves.

Thus, even accepting that the present classification of the Volutidae could be partly wrong, there is obvious radular convergence between species of Fulgorarinae and Zidoninae, between species of Lyriinae and Fulgorarinae and between species of Scaphellinae and Cymbiinae (Figure 3). At the same time it must be acknowledged that the inclusion of some genera within some of these subfamilies is uncertain; for instance, *Festilyria* placed in the Fulgorarinae by WEAVER & DUPONT (1970) could belong to the Lyriinae and *Harpovoluta*, referred by these same authors to the Fulgorarinae, is a genus of uncertain position but with a radula of the Zidoninae-type.

BAYER (1971: 201 - 202) has also postulated some trends in the functional modification of the rachidian tooth of several subfamilies in the tropical western Atlantic.

In his opinion, the comblike multicuspid rachidian tooth in *Voluta* (Volutinae) would indicate a tendency toward a tricuspid condition which by increasing curva-

ture of the basal plate and loss of the denticles would result in teeth such as those of *Zidona* (Zidoninae) and *Aurinia* (Scaphellinae).

Reduction of the lateral denticle (and the radula in general) would in turn result in teeth of the "scaphelloid" type conceivably serving a fang-like function. He further assumes that the teeth of *Volutomitra* have developed in "somewhat the same way" (?) as have those of *Odontocymbiola*.

We agree with Bayer that studies of the feeding behavior will aid the interpretation of the evolution of radular form but we do not agree on the trends. His adaptive sequence *Voluta* - *Lyria* - Zidoninae is conflicting since the Volutinae-type of rachidian tooth seems as specialized as the Scaphellinae-type or the Odontocymbiinae-type. Furthermore, the apparently logical sequence Zidoninae-Scaphellinae might have an alternative sequence if possible derivation from some members of the Cymbiinae is considered.

Figure 3 represents an arrangement of possible adaptive tendencies towards specialization of the radula of the Volutidae, but does not necessarily imply phylogenetic relationships. Nonetheless, it agrees well with at least the basic differentiation of subfamilies.

Accepting that the triserial radula is less specialized and postulating accordingly a derivation from radular types such as those found in the living Athletinae and some Calliotectinae, or similar ones, the volutids can be separated according to 3 main tendencies:

a) Decreased curvature of the basal plate  
as a result of widening

The Volutinae represent the culmination of this adaptive line which also includes the Lyriinae, the Fulgorarinae (at least in part) and the Calliotectinae. It does not seem mere coincidence that all these subfamilies have opercula (Figure 3, a).

### Explanation of Figures 12 to 16

*Proscaphella domeykoana* (Philippi, 1887)

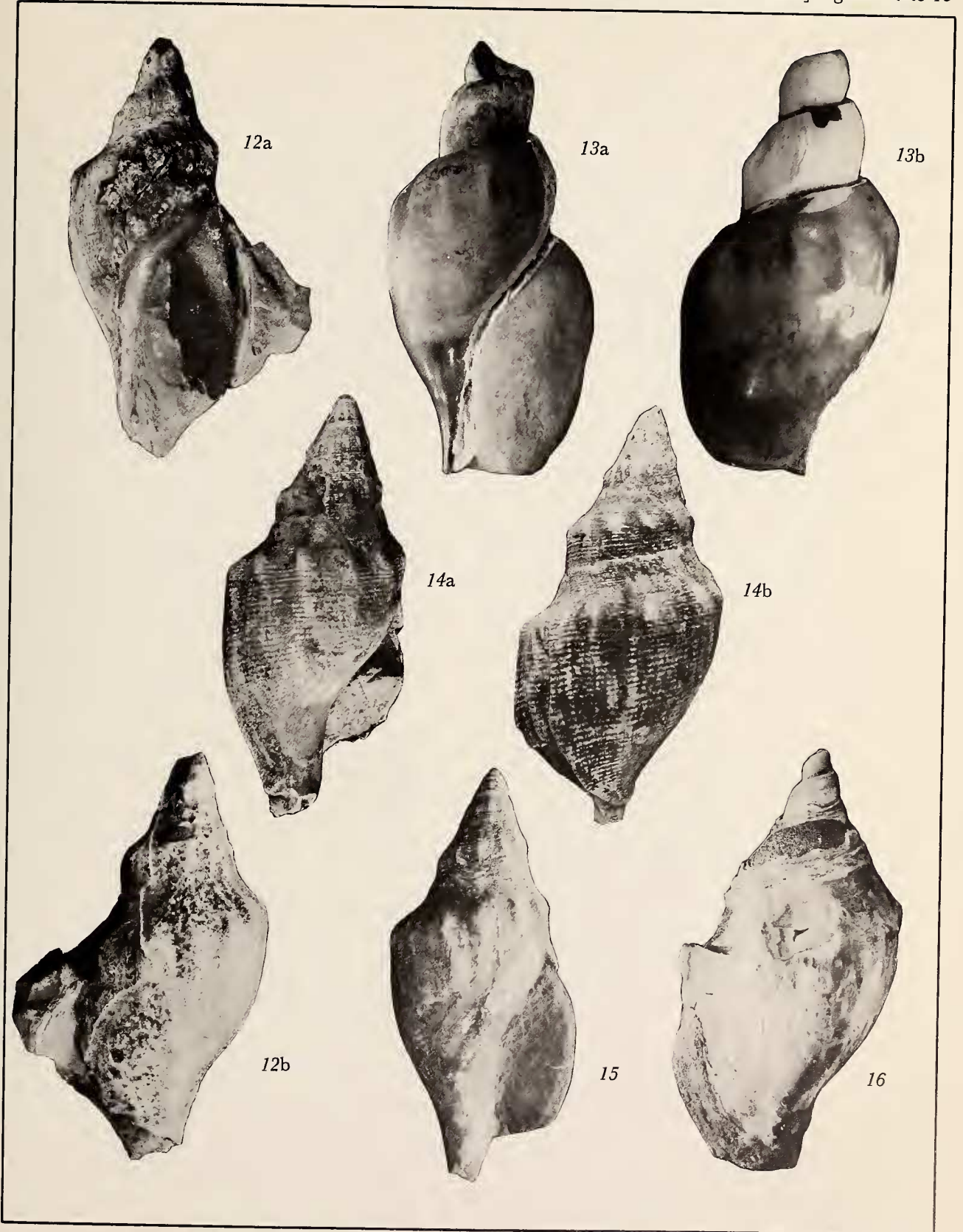
Figures 12a, 12b: MNHN 102; Lower Miocene, Matanzas; 90 mm high

Figures 13a, 13b: MNHN 110; Upper Cretaceous?, Quiriquina; 69.5 mm high

Figures 14a, 14b: MNHN 111; Lower Miocene, Navidad; 76 mm high

Figures 15a, 15b: Lectotype MNHN 113; Lower Miocene, Navidad; 85 mm high

Figures 16a, 16b: MNHN 111; Lower Miocene, Navidad; 92 mm high





**b) Increased curvature of the basal plate  
with reduction of the lateral denticles**

This adaptive line presents in turn 2 definite trends (Figure 3, b). One, characterized by a moderate development of the curvature of the basal plate and moderate reduction of the lateral cusps, is typical of the Zidoninae. The other, with moderate to total reduction of the lateral cusps, is found in the Scaphellinae and some Cymbiinae (except for possible relationships with the Scaphellinae, as discussed above, the tricuspid teeth of the Cymbiinae seem too diversified to allow an analysis of possible intergeneric trends and relationships with the other subfamilies).

**c) Inverted curvature of the basal plate  
with development of fang-like teeth**

This peculiar trend seems to be typical for the Odontocymbioliinae.

Based on radular resemblance, WEAVER & DUPONT (1970: 126, 131) included in this subfamily the following genera: *Volutoconus* Crosse, 1871; *Tractolira* Dall, 1896; *Miomelon* Dall, 1907; and *Odontocymbiola* Clench & Turner, 1964; however, the interrelationships of these taxa are by no means clear.

*Volutoconus*, previously included within the oviparous Cymbiinae by Pilsbry & Olsson could, in our opinion, be referred with equal validity to the Scaphellinae.

The monotypic genus *Tractolira* Dall is only known from the original type series. The teeth in this genus were characterized by WEAVER & DUPONT (1970) as having "three fang-like cusps;" however, DALL (1907: 366) stated that its dentition "... is marked by the same tusk-like cusps which are found in *Miomelon*." Unfortunately, the teeth of *Tractolira* have not been figured, but Dall's description does not suggest similarity with the radular teeth typical for *Odontocymbiola* or *Volutoconus*. Indeed, he assorted them with those of *Miomelon* in a different type, characterized by "tusk-like cusps" (DALL, *op. cit.*: 343). Moreover, the shell is definitely closer to *Miomelon* than to *Odontocymbiola* or *Volutoconus*, and the animal is described by Dall as being blind, a feature shared by the abyssal *M. philippiana*.

Thus, the sequence shown in Figure 3, c may not represent an adaptive sequence at all and the genera *Miomelon* and *Tractolira* could rather constitute a different phyletic line.

Undoubtedly, thorough studies of functional anatomy, morphology, and ecology are necessary to substantiate any conclusion.

**2. Fossil Species Referred  
to *Miomelon* and *Proscaphella***

POWELL (1951: 163) has called attention to the affinities between the genus *Miomelon* and the New Zealand *Palomelon* Finlay, 1926, stating however, that the latter "... lacks the channelled suture, has a more clearly defined fasciole and no spiral sculpture." He also remarks that DALL (1907) quoted *M. philippiana* as congeneric with the Chilean Tertiary *Voluta d'orbignyana* Philippi, *V. domeykoana* Philippi, *V. gracilis* Philippi, *V. indurata* Conrad, and *V. triplicata* Sowerby.

Actually, DALL (1889) originally reported that all the species from the Tertiary strata of Chile mentioned above formed one group to which his *Volutilithes philippiana* could be added as the only living representative. Mentioning the great resemblance of *V. philippiana* to *Voluta gracilis*, he suggested that in a large series of samples they "... would prove to be hardly specifically distinct." He also cautioned that the west American Tertiary group in question might turn out to be a single species, but suggested that specimens of these various species must be studied in order to prove this. Later (DALL, 1907), he decided to separate his new species and the Chilean fossil volutes from *Volutilithes*, proposing to group them as the new "section" *Miomelon* of the genus *Adelomelon*. The only fossil species included were *Voluta triplicata*, *V. domeykoana*, and he added "... perhaps also *Voluta d'orbignyana* Philippi."

The same year that DALL (1907) proposed the name *Miomelon*, VON IHERING (1907: 207) proposed the new genus *Proscaphella* to include some of the fossil volutids described by himself (*op. cit.*), PHILIPPI (1887) and ORTMANN (1902) from the Tertiary strata of Chile and Argentinian Patagonia. He selected *Voluta gracilior* von Ihering, 1896 (= *Voluta gracilis* Philippi, 1887, non LEA, 1883, nec SWAINSON, 1842) from the Patagonian formation of Santa Cruz, Argentina, as the type of the genus, renaming it *Proscaphella gracilior* (von Ihering, 1896).

The original diagnosis of *Proscaphella* was as follows:

"Ce genre est intimement lié à *Cymbiola* Sws., s'en distinguant par la sculpture qui consiste en des plis longitudinaux et en des sillons et crêtes spirales. La spire est plus ou moins allongée, la forme de la coquille est fusiforme, la columelle est munie de trois plis, dont quelquefois le postérieur est obsolète. La protoconche est lisse, scaphelloïde, et un peu moins épaisse que dans *Cymbiola*. Le nombre des plis est en général de 14-16 par tour."

In addition to the "type-species", the other species included in the genus were: *Proscaphella cossmanni* von Ihering, 1907; *P. quemadensis* (von Ihering, 1896), *P.*

*orbignyana* (Philippi, 1887), *P. petersoni* (Ortmann, 1900), all from the Argentinian Patagonia, and *P. domeykoana* (Philippi, 1887), *P. indurata* (Conrad, 1849) and *P. triplicata* (Sowerby, 1846) from Chile.

Later, informed of the publication of Dall's "section" of *Miomelon*, VON IHERING (1914: 110) listed *Proscaphella* as a synonym of *Miomelon* and considered the latter as a subgenus of *Cymbiola*. Unaware of von Ihering's decision or, perhaps, because of convenience some authors have continued to use the name *Proscaphella* for the fossil species (FERUGLIO, 1949; HOFFSTETTER *et al.*, 1956). This arrangement is shared in the present paper, but justified on very different grounds.

Comparison of the description and figures of some of these fossil species with living species of *Miomelon* shows differences in several shell characters. Although the soft parts and the radula of the fossil species cannot be known, the shell differences justify their separation in a different taxon for which the name *Proscaphella* is available. Two of the fossil species, *i. e.*, *Proscaphella gracilior* von Ihering, 1907, and *P. cosmanni* von Ihering, 1907, somewhat resemble the species of *Miomelon* and could be fossil representatives of the latter. However, they have more features in common with *Proscaphella* and are here treated as such.

MÖRICKE (1895: 571) has called attention to the limited distribution and high diversity reached by the fossil "volutes" of the Tertiary strata of central Chile and Patagonia, suggesting affinities with a group of fossil to Recent species from New Zealand.

The relationships with the fossil Scaphellinae from New Zealand and Australia were further discussed by ORTMANN (1902: 297 - 303) and VON IHERING (1897, 1899, 1907), but they began to be properly understood only after the works of MARWICK (1926); FINLAY (1927, 1930) and IREDALE (1934, 1937) were published, pointing to 2 very different faunistic complexes. Thus, the genera *Waihaeia*, *Mauithoe*, *Spinomelon*, *Teremelon*, *Pachymelon*, *Alcithoe*, *Palomelon* among others, mostly of medium size and with a high number of columellar plicae, seem to have little in common with the large-sized fossil species discussed here. On the other hand, it is obvious that the traditional views on the supraspecific categories grouping the fossil South American "volutes" have been oversimplified, and that a great deal more paleontological work is necessary to fully understand their taxonomy and phylogeny. For example, the Recent genus *Miomelon* might be more closely related to the fossil species than we suggest in this paper; nonetheless, the separation of the fossil species in a different taxon seems justified. It is on this basis that we propose to revalidate von Ihering's genus *Proscaphella*, redescribed below.

*Proscaphella* von Ihering, 1907

*Proscaphella* von Ihering, 1907, Anal. Mus. Nas. Buenos Air. 7 (3): 205. Type species: *Proscaphella gracilior* von Ihering, 1907: by OD

**Geographic Range:** Chile and Argentina (to Brazil?)

**Stratigraphic Range:** Cretaceous: Quiriquina Island, Chile

Tertiary: Chiloé, Lebu, Mocha Island and Navidad (Navidad Formation), Chile; Santa Cruz, Yegua Quemada and Cabo Tres Puntas (Patagonian Formation), Argentina

**Diagnosis:** Shell thick, oval to sub-fusiform, medium to large in size (up to 160mm in height). Spire more or less elevated, seldom as long as the aperture. Protoconch smooth, scaphelloid. Sculpture characterized by a fine wavy filigree formed by the criss-crossing of axial, flat costae and striae with extremely numerous flat spiral costellae and striae. With few but strong axial folds (ribs) forming large, round or sharp nodules on the shoulders; folds sometimes reduced or obsolete on the body whorl. Often with a ramp below the suture marked only by spiral sculpture. Aperture sub-quadrangular. Columella with 2 or 3 strong plait; siphonal canal long, deep, with a weak fold-like basal fasciole. There are 11 to 16 folds on the last whorl.

**Remarks:** From above, the main shell differences between *Miomelon* and *Proscaphella* are the following:

<i>Proscaphella</i> von Ihering	<i>Miomelon</i> Dall
1) Shell medium to large, up to 160mm in height	1) Shell medium sized, up to 90mm in height
2) Axial costae not numerous, with large nodules	2) Densely axially folded, without nodules
3) Sculpture characterized by a fine, wavy filigree, formed by the criss-crossing of the radial flat costae and striae with the extremely numerous flat spiral costellae and striae	3) Axial and spiral sculpture not forming a fine and wavy reticulum or filigree

VON IHERING (1907: 206) remarked that in the species from Chile the axial folds of the last whorls are abruptly interrupted at a certain distance above the whorl shoulder; however, this also occurs in the species of *Miomelon*, in other volutids, some turrids, buccinids, etc., and cannot be used as a distinctive feature. It seems doubtful that a group of Patagonian species could differ only in that feature from relatives of an otherwise very similar taxon.



The detailed examination of samples of some of the fossil species confirms the differences indicated above.

Thanks to the kindness of Mrs. Valeria Ascárate, geologist in charge of the Paleontological Collections of the Museo Nacional de Historia Natural, Santiago, Chile, we received on loan the types of the fossil species mentioned by PHILIPPI (1887) in his "Fósiles Terciarios i Cuartarios de Chile." In addition, samples existing in the Paleontological Collections of the Instituto Central de Biología, Universidad de Concepción, Concepción, Chile, were provided by Sr. Lajos Biró. They are listed herein according to the following abbreviations:

MNHN = Museo Nacional de Historia Natural, Santiago  
MZICB = Museo de Zoología, Instituto Central de Biología

CP = Colección Paleontológica

Figures 4 to 21 (on the 4 Plates) show frontal and dorsal views of the types and other specimens studied, and their characteristics are discussed according to the sequence originally followed by PHILIPPI (1887).

*Proscaphella dorbignyana* (Philippi, 1887)

(Figures 11a, 11b)

*Voluta dorbignyana* Philippi, 1887, Fós. Terc. Cuart. Chile: 65, pl. 7, fig. 7; VON IHERING, 1899, Neu. Jahrb. Miner. 2: 33; ORTMANN, 1902, Reprt. Princeton Univ. Exp. Patagon. 4 (2): 230, pl. 36, figs. 1b-1e

*Voluta d'orbignyana*. DALL, 1889, Proc. U. S. Nat. Mus. 12: 314; 1907, Smithsonian. Misc. Coll. 3 (3): 365

*Proscaphella orbignyana*. VON IHERING, 1907, An. Mus. Nac. Buenos Aires (3) 7: 208

*Proscaphella dorbignyana*. VON IHERING, 1907, An. Mus. Nat. Buenos Aires (3) 7: 101; FERUGLIO, 1949, Descrip. Geol. Patagon.: 264

*Cymbiola (Miomelon) orbignyana*. VON IHERING, 1914, Notas Rev. Mus. Paulista 1 (3): 110

*Adelomelon d'orbignyana*. DALL, 1907, Smithsonian. Misc. Coll. 3 (3): 365

*Voluta triplicata* VON IHERING, 1899, Conch. Patag. Form.: 33 (non Sowerby, 1846)

**Type Locality:** Santa Cruz, Argentina (PHILIPPI, 1887)

**Stratigraphic Range:** Tertiary: Middle Patagonian (Patagonian Formation) (VON IHERING, 1907)

**Original Description:** "Testa oblongo-fusiformis, transversim sulcato-striata; anfractus parum convexi, posterius undatim plicati, plicis in ultimo demum evanescentibus; anfractus ultimus maximus spiram saltem ter, aequans.—Longit. 15-16 cent., crass. 7 cent." (PHILIPPI, 1887).

**Remarks:** The species was based on only one specimen measuring 150 - 160mm in height and 70mm in width.

The type represented in Figures 11a, 11b, is in the Museo Nacional de Historia Natural, Santiago, and measures 118mm in height and 67mm in width. Unfortunately, the specimen has lost the shell matrix and, consequently, the details of sculpture shown in Philippi's original figure cannot be observed. In the remaining internal mold the axial folds appear almost obsolete in the last whorl, averaging 8 to 9. The columellar plaits cannot be seen.

As pointed out by VON IHERING (1899) and ORTMANN (1902), this species is characterized by its elongated mouth and by the tendency of longitudinal ribs to disappear on the last whorls. In large individuals, and particularly in the case of the type, the last whorl is almost completely without folds (ribs) or marked by only a few rather obsolete ones.

Lacking well preserved specimens, and not having a sufficiently large series to study variation, it is difficult to define the species. This probably explains why this and allied species have often been misidentified. For instance, ORTMANN (1902) listed *Voluta triplicata* von Ihering (non Sowerby) as a synonym of *Proscaphella dorbignyana*, a conclusion accepted by VON IHERING himself (1907). Moreover, one of the specimens figured by ORTMANN (1902: fig. 1a of *V. dorbignyana*) seems to belong to another species, as pointed out by VON IHERING (1907), who excluded it from the synonymy of *P. dorbignyana* and listed it as *Cymbiola*. We agree with von Ihering in considering that specimen a different species, but we cannot with certainty assign it to any of the fossil volutids of Patagonia. It was probably on the basis of this specimen that Ortmann remarked that *P. dorbignyana* corresponds closely to the living *Adelomelon ancilla* and that it might be its ancestral form. Apart from this individual which resembles *A. ancilla*, there is no valid argument to consider *P. dorbignyana* as its ancestor and, for that matter, its relationships to *Adelomelon* and *Odontocymbiola* from southern South America are as equivocal as those to *Miomelon* or to other genera of the Volutidae.

*Proscaphella domeykoana* (Philippi, 1887)

(Figures 12a to 16b; Figure 21)

*Voluta domeykoana* Philippi, 1887, Fós. Terc. Cuart. Chile: 66, pl. 8, fig. 4; DALL, 1889, Proc. U. S. Nat. Mus. 12: 314; STEINMANN *et al.*, 1895, Beitr. Geol. Patag. 1 (3): 22, 24; MÖRIKE, 1895, Beitr. Geol. 1 (4): 551, 571; FUENZALIDA, 1938, Bol. Min. Petrol. 8 (79): 86; Idem, as "Separata con correcciones." Imp. Mus. Nac. Hist. Nat. Santiago; TAVERA, 1942, An. 1<sup>er</sup> Congr. Panam. Ing. Min. Geol. 2 (1): 602, 604, 606, 613; TAVERA & VEYL, 1958,